

Allometric growth and performance of the gastric caeca of *Zonocerus variegatus* (L.) (Orthoptera: Pyrgomorphidae)

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Abstract: The allometry, growth and activities of the gastric caeca of *Zonocerus variegatus* (L.) were determined to find out the functions of its posterior caeca which are unknown. This was done by dissecting out the gut and measuring the main gut regions and the gastric caeca in the six nymphal stages and adult. The gut consists of three main regions; the crop, ventriculus, with gastric caeca attached at anterior rim, and the hindgut. Each set of caeca consists of a long anteriorly pointed arm and a short posteriorly pointed arm. The growth of the caeca relative to the main gut was allometric. The anterior caeca had higher growth ratios than the posterior caeca and both were highly correlated. The relationship between gut and caeca mean length was highly significant. The mean gut length and age were significantly correlated with growth rate exponent < 1 indicating a decreasing growth increment with age. The mean caeca length and age were highly correlated with growth exponent > 1 indicating an increasing growth with age. Females had higher mean lengths than males and this was highly significant ($P < 0.05$). Males had higher growth ratios than females except at growth centres. The growth patterns of the caeca for wet and dry seasons were similar with a single growth centre. But the mean length of the caeca was significantly different between wet and dry season's insects from the fourth instar to adult. The posterior caeca was considered a complementary structure to the anterior caeca. They perform the same function of digestion and absorption of food. The posterior caeca is concluded additional device to increase the surface area of the ventriculus to cope with low nutrient status of herbivory.

Key words: *Zonocerus variegatus*; gastric caeca; growth gradient; function

1 INTRODUCTION

The occurrence of gastric caeca in insects is restrictive. It is common among solid feeders mostly acridids. Its absence in most insects is considered to be of evolutionary importance in avoiding accumulation of noxious wastes in anterior midgut (Terra, 1990). The caeca exist as unilobed or bilobed consisting of anterior and posterior arms. The posterior arms may be reduced to tubercles or are absent (Uvarov, 1966). They vary in shapes, numbers and length and may be located at different points of the gut (Areckul, 1957). Barnhart (1961) reported variations in caeca size from the usual condition to a reduced non-branched dough nut like process. In oligophagous insects from graminivorous subfamilies, caeca are absent (Bernays, 1981). In

Rhyncosciara americana, there are two gastric caeca which are about 30% of the ventricular length and their diameter is similar to the smaller ventricular diameter (Ferreira *et al.*, 1993). In *Schistocerca gregaria* (Dow, 1981a; Bernays, 1981), there are six gastric caeca which vary systematically in size, the dorsal caeca being the largest. In Bavarian acridids (Kaufmann, 1965), six gastric caeca are reported. They differ morphologically mostly in the proportions of the anterior and posterior lobes. No differences were noted between the sexes, or between the various nymphal instars in any of the species examined. In some insects, the caeca appear only in some stages of the insect development. In mosquito larvae, gastric caeca had been observed but not reported in adult mosquitoes (Volksmann and Peters, 1989).

The anterior caeca arms have been identified as

the main site for food absorption (Treherne, 1957, 1958a, b, and c; Berridge, 1970; Dow, 1981a). The functions of the posterior caeca arms are uncertain (Bernays, 1981), even though in *Abracris flavolin-eata*, it is assumed to have the same digestive functions with the anterior caeca but on a small scale due to the small size (Marana *et al.*, 1997). The uncertainty is probably caused by some structural variations in the posterior caeca arms among different insects. For instance, the pockets found in the posterior caeca of *S. gregaria* were not found in *Zonocerus variegatus* (Bernays, 1981). Secondly there are various size and shape of the posterior caeca in many insects and it is more developed in forbivorous than graminivorous insect species (Chapman, 1988). It is therefore presumed that the function of the posterior caeca will be varied according to variations in sizes, shapes and structure among insects. The study was therefore carried out to determine the functions of the posterior gastric caeca in *Zonocerus variegatus* (L.) and to increase the knowledge on the digestive physiology of the subject. It was therefore designed to include the morphometric measurements of the caeca arms in the six nymphal stages and adult, for males and females in dry and wet seasons.

2 MATERIAL AND METHODS

2.1 Collection of the insects

The insects were collected from an uncultivated thicket of *Chromolaena odoratum* inside the International Institute for Tropical Agriculture (IITA) in Ibadan. The collection was made between October and January for dry season and between March and September for wet season. Each stage was collected as the insects developed into the different developmental stages. Separation into males and females was done using ovipositor.

2.2 Measurement of gut lengths

The collected insects were carried in insect cage (300 cm × 300 cm × 300 cm) to the laboratory. The insect were killed using ether and dissected. Lengths of dissected out gut regions were measured. The regions were crop, ventriculus, hindgut, anterior caeca (Ac) and posterior caeca (Pc). Measurements of instars I

– III were done with stage micrometer on a dissecting microscope. Instars IV – adults were measured with transparent ruler. 100 insects were measured for each stage giving 700 insects in sum.

The relationship between gut length and caeca length was estimated through base-10 log transformation of gut-caeca data pairs and ordinary least squares linear regression. The power function representing this relationship is

$$\text{Log } C = \log a G^b \quad (1)$$

where C is the length of allometrically growing caeca, b is the theoretical value of C when the standard measurement (Gut) (G) equals unity and is called initial growth index. ' a ' is the constant at which G grows in relation to the C and is called the growth ratio. In this relationship if $a = 1.0$ growth rate is constant and equal to the initial growth constant (isometric), otherwise it is negative (< 1.0) or positive (> 1.0) allometric growth.

3 RESULTS

3.1 Morphometry

Three main regions (crop, ventriculus and hindgut) were observed between post buccal regions and anal opening. At the anterior rim of the ventriculus are six diverticulae consisting of anteriorly and posteriorly pointed arms. The caeca taper distally and are held closely to the surface of the gut. The anterior arms extend to the crop wall while the posterior arms extend to the anterior half of the ventricular wall. The mean lengths of the anterior and posterior caeca at various developmental stages of the insect are presented on Table 1. The Ac is longer than the Pc in all the stages. The growth of the caeca in relationship to the gut is allometric. The allometry patterns for the two sets of caeca arms were similar as shown by their growth gradients (Fig. 1a, b). The posterior caeca had lesser values for ' a ' (growth ratio), hence lesser growth gradient than the anterior arm. The ' a ' values for both structures differed significantly in a similar manner from zero and unity.

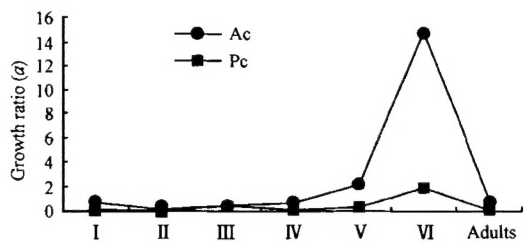


Fig. 1a Growth gradients of gastric caeca of dry season, *Z. variegatus*, first instar to adult

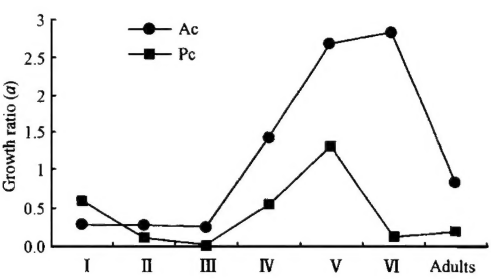


Fig. 1b Growth gradients of gastric caeca of wet season, *Z. variegatus*, first instar to adult

Ac = anterior; Pc = posterior caeca. The same for the following figures.

Table 1 Mean lengths of the gut regions of *Z. variegatus* (mean \pm SD) (mm)

Instar	N	Season	Anterior caeca	Posterior caeca	Foregut	Midgut	Hingut
I	100	Wet	1.11 \pm 0.58	0.33 \pm 0.09	2.63 \pm 0.53	1.89 \pm 0.38	2.23 \pm 0.26
	100	Dry	1.03 \pm 0.24	0.35 \pm 0.11	2.60 \pm 0.56	2.13 \pm 0.41	2.11 \pm 0.31
II	100	Wet	1.61 \pm 0.32	0.59 \pm 0.15	3.20 \pm 0.60	2.77 \pm 0.61	2.51 \pm 0.44
	100	Dry	1.47 \pm 0.17	0.64 \pm 0.17	3.30 \pm 0.55	2.80 \pm 0.49	2.69 \pm 0.30
III	100	Wet	2.02 \pm 0.40	0.83 \pm 0.31	3.68 \pm 0.53	3.42 \pm 0.64	2.83 \pm 0.33
	100	Dry	2.16 \pm 0.48	1.10 \pm 0.32	3.72 \pm 1.00	3.57 \pm 0.75	3.56 \pm 0.56
IV	100	Wet	2.98 \pm 0.67	1.46 \pm 0.45	5.66 \pm 1.27	4.84 \pm 0.94	4.43 \pm 0.79
	100	Dry	3.38 \pm 0.67	1.89 \pm 0.51	5.98 \pm 1.30	4.76 \pm 0.96	5.17 \pm 0.75
V	100	Wet	4.05 \pm 0.69	2.32 \pm 0.45	7.87 \pm 1.36	6.68 \pm 0.93	5.72 \pm 0.81
	100	Dry	4.64 \pm 0.96	2.83 \pm 0.66	7.64 \pm 1.46	6.32 \pm 1.31	6.49 \pm 1.07
VI	100	Wet	5.24 \pm 1.04	3.32 \pm 0.80	9.41 \pm 1.77	8.99 \pm 1.69	7.74 \pm 1.38
	100	Dry	6.84 \pm 1.23	4.08 \pm 1.23	10.19 \pm 1.88	8.61 \pm 1.77	8.14 \pm 1.58
Adult	100	Wet	6.14 \pm 1.20	4.43 \pm 1.09	10.79 \pm 2.02	11.78 \pm 1.92	8.67 \pm 1.05
	100	Dry	8.43 \pm 1.90	5.04 \pm 1.27	12.76 \pm 2.28	10.20 \pm 3.25	9.27 \pm 1.35

Estimates of relationships between Ac and Pc indicate high correlation between these structures ($r = 0.995$, $n = 7$ for dry season and 0.989 , $n = 7$ for wet season, $P < 0.05$) (Fig. 2a – d).

3.2 Caeca-gut relationships

The relationships between gut and caeca lengths were highly significant, for Ac ($r = 0.998$, $n = 7$, $P < 0.05$) and Pc ($r = 0.993$, $n = 7$, $P < 0.05$) and their respective equations are:

$$\text{Log AcL} = 0.110 + 1.220 \text{ Log GL} \tag{2}$$

$$\text{Log PcL} = 0.017 + 1.646 \text{ Log GL} \tag{3}$$

Mean gut length (Lt) and age were significantly correlated ($r = 0.956$, $n = 7$, $P < 0.05$) according to the power function:

$$Lt = 5.515t^{0.815} \tag{4}$$

Their growth rate exponent was < 1 indicating a decreasing growth increment with age. This is further confirmed by little or inverse relationships: age vs length gain (LG) ($r = -0.180$) and age vs growth

rate (GR) ($r = -0.597$, $n = 7$, $P < 0.05$) from Table 2. The functional equations for these relationships are respectively:

$$LG = 3.367 (t^{0.149})^{-1} \tag{5}$$

$$GR = 5.518 (t^{0.186})^{-1} \tag{6}$$

The mean caeca lengths and age were also significantly correlated: ($r = 0.972$, $n = 7$, $P < 0.05$) for posterior caeca. The power function indicating these relationships are:

$$Lt = 0.867t^{1.013} \text{ Ac} \tag{7}$$

$$Lt = 0.272t^{1.390} \text{ Pc} \tag{8}$$

Their growth rate exponents were > 1 indicating an increasing growth with age (instar). These were also supported by their inverse relationships: Age vs Ac length gain (AcLG) ($r = 0.491$, $n = 7$, $P < 0.1$) and age vs Ac growth rate GR ($r = -0.051$). Expressed by the following equations:

$$\text{AcLG} = 0.640 t^{0.323} \tag{9}$$

$$\text{AcGR} = 0.867t^{0.013} \tag{10}$$

Age *vs* Pc length gain (PcLG) ($r = 0.569$, $n = 7$, $P < 0.05$) and age *vs* Pc growth rate (PcGR) ($r = 0.833$, $n = 7$, $P < 0.05$). The corresponding

equations representing these relationships are:

$$PcLG = 0.238t^{0.747} \tag{11}$$

$$PcGR = 0.271t^{0.393} \tag{12}$$

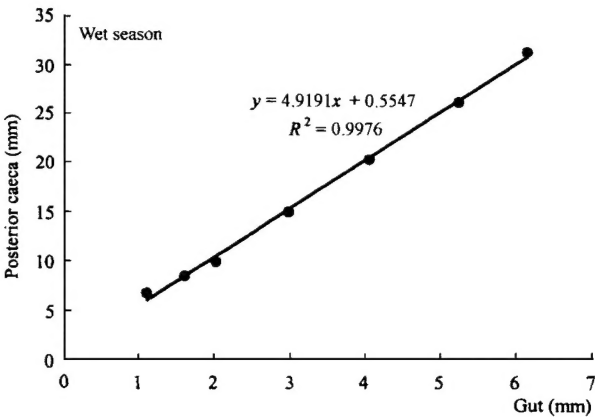


Fig. 2a Mean length relationship between gut and posterior gastric caeca of *Z. variegatus* first instar to adult in wet season

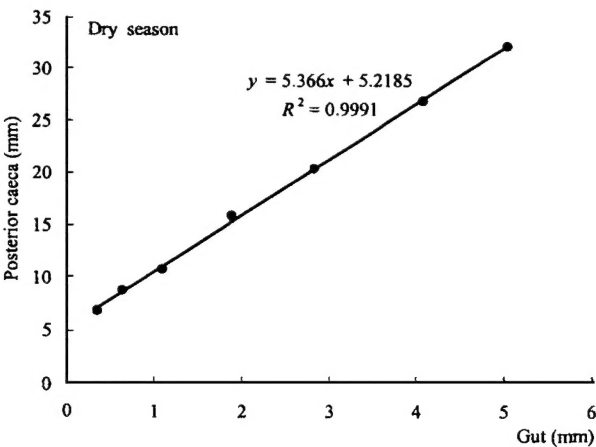


Fig. 2b Mean length relationship between gut and posterior gastric caeca of *Z. variegatus* first instar to adult in dry season

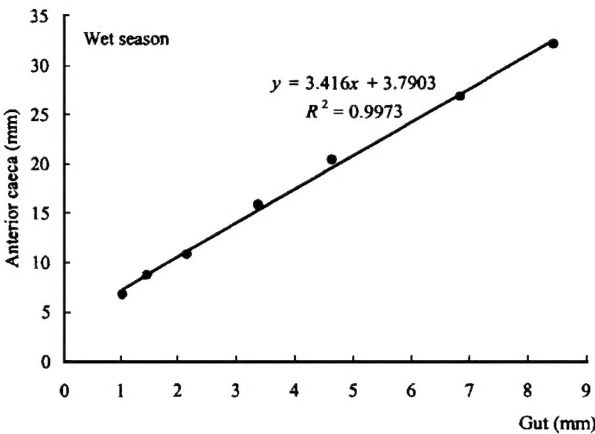


Fig. 2c Mean length relationship between gut and anterior gastric caeca of *Z. variegatus* first instar to adult in wet season

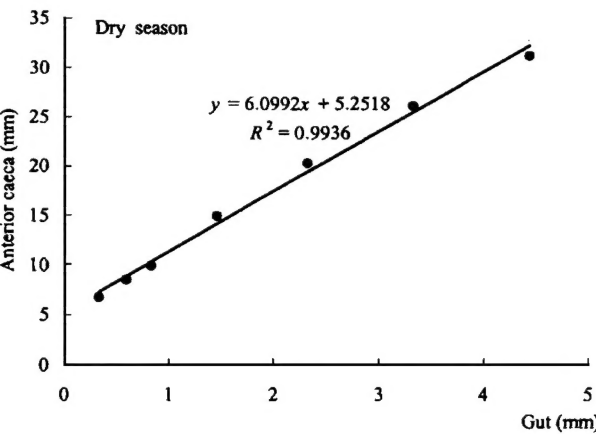


Fig. 2d Mean length relationship between gut and anterior gastric caeca of *Z. variegatus* first instar to adult in dry season

Table 2 Length, length gain and growth rate of *Z. variegatus* gut, anterior and posterior caeca at different age

Instar	Gut			Anterior caeca			Posterior caeca		
	Mean Gut	Mean Length	Mean Growth	Mean Gut	Mean Length	Mean Growth	Mean Gut	Mean Length	Mean Growth
	Length	Gain	Rate	Length	Gain	Rate	Length	Gain	Rate
I	6.80	6.80	6.80	1.07	1.07	1.07	0.34	0.34	0.34
II	8.65	1.85	4.33	1.54	0.47	0.77	0.62	0.28	0.31
III	10.39	1.74	3.46	2.09	0.55	0.70	0.97	0.35	0.32
IV	15.42	5.03	3.86	3.13	1.04	0.78	1.68	0.71	0.42
V	20.36	4.94	4.07	4.35	1.22	0.87	2.58	0.90	0.52
VI	26.54	6.18	4.42	6.04	1.69	1.01	3.70	1.12	0.62
Adult	31.74	5.20	4.53	7.29	1.25	1.52	4.74	1.04	0.68

3.3 Variations in caecal means length with sex

There was an outstanding significant difference in the caecal lengths between male and female *Z. variegatus* (Table 3). In first, sixth instars and adults females have higher mean length for Ac and Pc in both dry and wet seasons than males ($P < 0.05$). This is prominent in the sixth instar and adults. Between the second and fifth instars there is no significant difference between males and

females.

The gastric caeca of both sexes show allometric growth (Figs. 3a, b; 4a, b). Growth of the males Pc in wet season was negatively allometric (Fig. 4b). The growth ratio values were generally lower in females than in males except at growth centres and in third, fourth instars and adults as shown by their growth gradients.

Table 3 Differences in the means lengths of caeca of males and females *Z. variegatus* in wet and dry seasons (mean \pm SD) (mm)

Instar	Anterior Caeca				Posterior Caeca			
	Dry Season		Wet Season		Dry Season		Wet Season	
	Male	Female	Male	Female	Male	Female	Male	Female
I	0.66 \pm 0.20	0.74 \pm 0.23	0.74 \pm 0.20	0.80 \pm 0.28	0.22 \pm 0.09	0.25 \pm 0.09	0.23 \pm 0.76	0.26 \pm 0.09*
II	1.35 \pm 0.40	1.37 \pm 0.43	1.39 \pm 0.58	1.38 \pm 0.36	0.58 \pm 0.27	0.66 \pm 0.25	0.53 \pm 0.23	0.51 \pm 0.15
III	2.93 \pm 0.81	2.39 \pm 0.83	2.04 \pm 0.53	2.11 \pm 0.59	1.21 \pm 0.53	1.27 \pm 0.49	0.85 \pm 0.29	0.86 \pm 0.27
IV	5.26 \pm 1.51	5.19 \pm 1.41	4.39 \pm 1.27	4.59 \pm 1.45	3.00 \pm 1.07	3.15 \pm 1.15	2.18 \pm 0.89	2.30 \pm 0.94
V	9.62 \pm 2.61	9.56 \pm 2.62	8.12 \pm 1.39	8.27 \pm 1.57	5.73 \pm 1.93	5.92 \pm 1.77	5.30 \pm 1.89	4.74 \pm 0.97
VI	16.89 \pm 3.71	19.18 \pm 4.05	13.13 \pm 2.98	14.48 \pm 4.79	10.19 \pm 2.97	11.53 \pm 3.06	8.36 \pm 2.61	9.30 \pm 2.85*
Adult	21.95 \pm 4.64	26.78 \pm 5.92	17.71 \pm 3.54	20.43 \pm 4.79	13.59 \pm 4.18	17.51 \pm 5.28	12.51 \pm 3.55	14.68 \pm 4.42*

* = Statistically significant ($P < 0.05$)

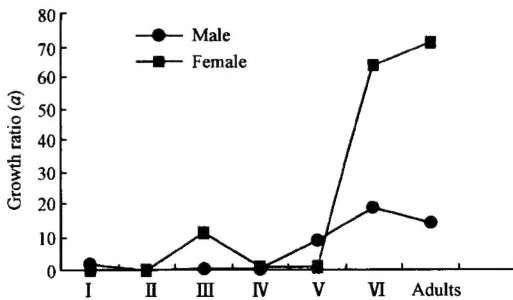


Fig. 3a Growth gradients of anterior gastric caeca of male and female *Z. variegatus* first instar to adult in dry season

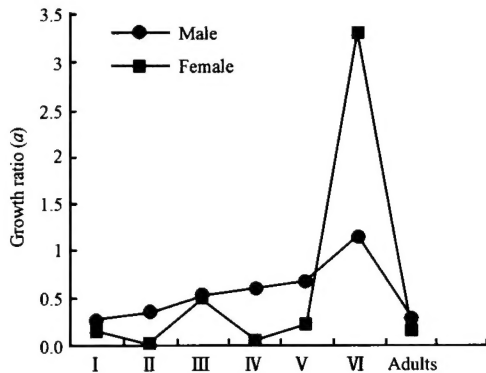


Fig. 3b Growth gradients of posterior gastric caeca of male and female *Z. variegatus* first instar to adult in dry season

Variations in caecal mean lengths with seasons were significantly different between wet and dry seasons from the fourth instar to adult (Table 4). Dry season had higher values than wet season. Each season had a

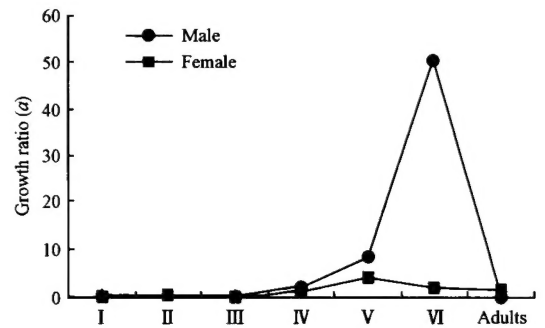


Fig. 4a Growth gradients of anterior gastric caeca of male and female *Z. variegatus* first instar to adult in wet season

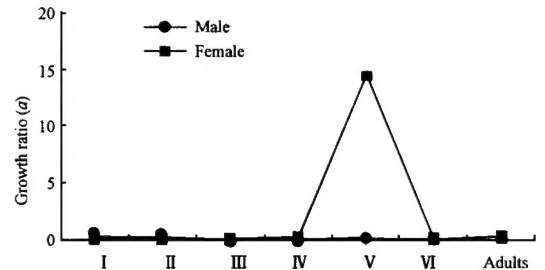


Fig. 4b Growth gradients of posterior gastric caeca of male and female *Z. variegatus* first instar to adult in wet season

single growth centre in anterior and posterior arms for both sexes (Figs. 3a, b; 4a, b). The growth patterns of the caeca for the two seasons were similar.

Table 4 Mean caecal length of caeca of *Z. variegatus* in wet and dry seasons (mean \pm SD) (mm)

Instar	Anterior caeca		Posterior caeca	
	Dry Season	Wet season	Dry season	Wet season
I	0.72 \pm 0.26	0.73 \pm 0.20	0.24 \pm 0.11	0.24 \pm 0.09
II	1.31 \pm 0.27	1.39 \pm 0.47	0.57 \pm 0.17	0.52 \pm 0.19
III	2.12 \pm 0.27	2.09 \pm 0.55	1.09 \pm 0.48	0.86 \pm 0.28
IV	5.31 \pm 1.42	4.50 \pm 1.37	3.15 \pm 1.17	2.23 \pm 0.92 *
V	8.45 \pm 2.02	8.26 \pm 1.48	5.58 \pm 1.79	4.87 \pm 1.47 *
VI	18.19 \pm 4.29	13.81 \pm 3.28	10.96 \pm 3.16	8.83 \pm 2.77 *
Adult	22.47 \pm 6.20	19.33 \pm 4.53	16.16 \pm 5.21	13.86 \pm 4.19 **

* = Statistically significant ($P < 0.05$).

3.4 Growth of the gut regions

The main gut regions were crop, ventriculus and hindgut. Crop seemed to have the greatest mean length especially in fed insects, followed by the ventriculus and hindgut (Table 1). Chi-squared test showed no significant difference in the mean length between the three main regions.

4 DISCUSSION

4.1 Anterior and posterior caeca

In *Z. variegatus* there are six units of gastric caeca. Each unit consists of an anterior arm and a posterior arm as observed in most acridids (Evans and Payne, 1964; Dow, 1981b; Bernays, 1981). Although in number, it resembles the gastric caeca of *S. gregaria*, morphologically they are different. The length of the posterior arm in *Z. variegatus* is shorter than the anterior arm whereas in *S. gregaria* it is the reverse (Bernays, 1981). This difference in length suggests that in such close species, the functions of the gastric caeca are likely different, of course physiologically they are not the same due to the absence of pockets in *Z. variegatus* caeca. The growth of the gastric caeca in relation to the gut length is allometric, this growth can be described as gut mediated. According to Fairbairn (1992), every allometry is presumed to arise from selection action primarily on overall body size but having secondary effects on other organs. With this assertion, the observed caecal allometry to full gut (target organ)

is presumed to be obtaining secondary but differential responses from anterior and posterior gastric caeca (non target organ). Further, allometry reveals that there is significant effect of body size on virtually every trait (Shine *et al.*, 1998). This suggests that growth is essentially related to many other physiological processes (Needham, 1943) and even height and age (Lee and Moss, 1995). The similar pattern observed in the anterior and posterior gastric caeca suggests a similar physiologic function in the two units. According to Worcester (1995), functional equivalence is suspected in the two caeca arms.

The two caeca arms highly correlate to the entire gut indicate closeness in function. The anterior caeca have been identified as the main site for food and water uptake (Treherne, 1957, 1958a, b and c; Berridge, 1970; Ferreira *et al.*, 1981; Dow, 1981 a and b), and the posterior arm (in locust) as site for water uptake and waste expulsion (Bernays, 1981). Our results on allometry and correlation suggest the two caeca arms to be highly related to the gut in their functions are digestive and absorptive structures.

4.2 Caeca absorption

Considering the anterior caeca alone as the main absorbing organ, it would be expected to have a proportional increase in its surface area with the body volume. The proportional increase is necessary for complete absorption because of the low nutrient value of herbivory resulting in bulky ingestions. But the allometry observed seems not to indicate this. It is therefore be-

lieved that there are other ways through which this efficiency could be achieved. In one way, the organ might be so efficient in absorption and compensate for large food digested despite its slower growth relative to the body as a whole. Also this efficiency could be attained through mechanisms such as dense microvilli, formation of gastric caeca, and crypts along the midgut epithelium (Richards and Davies, 1978). It could therefore be argued that posterior caeca are supplementary structures of the anterior gastric caeca to increase the surface area for food absorption in commensuration with the body volume. In support of this idea, Bermays (1981) identified pockets in the epithehim of posterior caeca of *Schistocerca* as sites for rapid water uptake from gut lumen to increase the speed and efficiency of digestion and absorption of food.

4.3 Growth relationship between gut and caeca

The growth of the caeca again was negatively allometric in all stages of development except at fifth and sixth instars which showed positive allometry. The peaks generally occurred in the sixth instar which is considered the growth centre and have higher growth ratios. These high values correspond with period or stages of greatest feeding activity of the insect (Modder and Singh, 1976). The negative allometry indicates period of low feeding activities when caecal functions are correspondingly low. At these stages (first to fourth instar), the insect feeds mostly or only on *C. odoratum* (Okere, 1980; Toye, 1982; Modder, 1984) and this food plant according to Modder and Tamu (1996) and Akpan (2000) retards growth of the insect, hence the negative allometry.

The growth rate of the main gut and the gastric caeca were inverse, gut decreases, gastric caeca increases with age. Smaller organs have higher growth rate than bigger ones due to the larger surface area-volume ratio of the smaller ones. The growth rate is correspondingly and comparatively higher in the Pc than the Ac. The growth of the main gut was progressively higher than it occurred in the caeca, from the first instar. At the fifth instar, it outpaced the caeca shifting the Pc away from the mid transverse line (Fig. 5). By the fifth instar, much growth of the main gut was attained

while in the caeca there was still more growth. Hence the outpacing of the gut by the caeca in the later instars returns the Pc to the mid-transverse line in the fifth instar. Much growth in the Pc than the main gut further extends the Pc across the line in sixth instar. Invariably, growth in the main gut stops earlier.

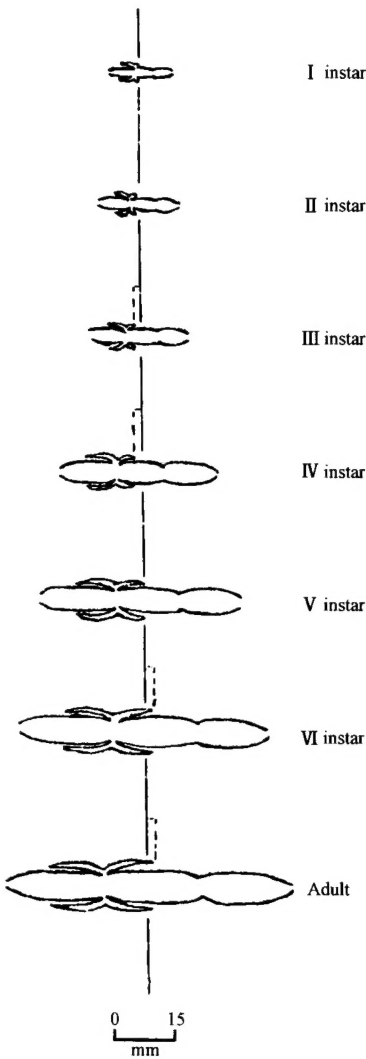


Fig. 5 Schematic representation of *Z. variegatus* gut from first instar to adult (the vertical line represents mid transverse line)

4.4 Length and age

Females had higher mean lengths than males at some stages. The difference at first instar shows the females to have started active growth process earlier than males. As growth progresses, the mean length of the caeca for both sexes was the same from second to fourth instar. It is then suggested that the males have been

eating more voraciously than females at those stages to offset the differences.

From the fifth instar, the insect assumes active and fast growth and reaches the peak in the sixth instar in line with increasing food demand for reproductive development as shown in Fig. 3. Strong (1967) reported that feeding activity at reproductive stage is higher than in the early stages. This is because of the eggs that are to be produced and laid by the insect (Shine *et al.*, 1998). Therefore most acridid example locusts begin to oviposit when maximum body weight has been attained (Cheu, 1952). *Z. variegatus* could then be suggested to be depositing enough food between fifth and sixth instar to enhance its attainment of maximum body weight (Modder and Singh, 1976), at the sixth instar for successful oviposition at adult stage. This is because when they emerge into adult stage according to Modder and Singh, they eat little to add to what was accumulated and attain the weight. As males spend little energy on reproductive activities, they consequently have less growth ratios.

Regarding the growth sequence of the insect then this could be summarized into three phases as; low growth phase (first to fourth instar), active growth phase (fifth and sixth instar) and little or no growth phase (adult stage).

From all the results obtained, the sixth instar of *Z. variegatus* stands out for two reasons. First, it has the greatest feeding activity and is therefore more devastating or inimical to crops than other instars. Secondly, it could be regarded as a transitory stage because of its transitory role between the somatic and reproductive growth phases of the insect.

4.5 Conclusions

The information obtained in this work further confirms the homogeneity of the dry and wet season populations of the insect. The observed difference in the mean lengths of the gastric caeca shown on Table 1 should be considered ecological. The availability and type of food plants can determine the growth of the insect. In the dry season, the insect are restricted to limited plants which may have low nutritional values because of the withering vegetation. As such the differences in growth

and sizes of the organ should be expected.

References

- Akpan B E, 2000. Morphology, histology and permeability studies of the ventriculus and gastric caeca of *Zonocerus variegatus* (L) (Orthoptera: Pyrgomorphidae). Ph. D Thesis University of Ibadan, Nigeria.
- Areckul S, 1957. The comparative internal larval anatomy of several genera of Scarabaeidae (Coleoptera). *Ann. ent. Soc. Am.*, 50: 563 – 577.
- Barnhart C S, 1961. The internal anatomy of the silver fish *Ctenolepisma campbelli* and *Lepisma saccharinum* (Thysanura: Lepismatidae). *Ann. ent. Soc. Am.*, 54: 177 – 199.
- Bernays E A, 1981. A specialized region of the gastric caeca in the locust, *Schistocerca gregaria*. *Physiol. Entomol.*, 6: 1 – 6.
- Berridge M J, 1970. A structural analysis of intestinal absorption. *Symp. Roy. Ent. Soc. Lond.*, 5: 135 – 150.
- Chapman R F, 1988. Variations in the size of the midgut caeca during the fifth instar of the grasshopper, *Schistocerca americana* (Drury). *J. Insect Physiol.*, 34: 329 – 335.
- Cheu S P, 1952. Changes in the fat and protein content of the African migratory locust, *Locusta migratoria migratoroides* (R & F). *Bull. ent. Res.*, 43: 101 – 109.
- Dow J A T, 1981a. Water, ions and nutrient uptake in the locust alimentary canal. Ph. D. Thesis, University of Cambridge.
- Dow J A T, 1981b. Ion and water transport in locust alimentary canal: evidence from in vivo electrochemical gradients. *J. exp. Biol.*, 93: 167 – 179.
- Evans N A, Payne P W, 1964. Carbohydrases of the alimentary tract of desert locust, *Schistocerca gregaria* (Forsk.). *J. Insect Physiol.*, 10: 657 – 674.
- Fairbairn D J, 1992. The origins of allometry: size and shape polymorphism in the common waters strider, *Gerris remigis* (Say) (Heteroptera: Gerridae). *Biol. J. Linn. Soc.*, 45: 167 – 186.
- Ferreira C, Ribeiro A F, Terra W R, 1981. Fine structure of the larval midgut of the fly *Rhyncosciara* and its physiological implications. *J. Insect Physiol.*, 27: 559 – 570.
- Ferreira C, Ribeiro A F, Terra W R, 1993. Ultrastructure and biochemical aspects of digestion in the imagoes of the fly *Rhyncosciara americana*. *Entomol. Exp. Appl.*, 66: 135 – 145.
- Kaufmann T, 1965. Observations on aggregation, migration and feeding habits of *Zonocerus variegatus* in Ghana (Orthoptera: Acrididae). *Ann. ent. Soc. Am.*, 58: 426 – 436.
- Lee P C, Moss C J, 1995. Statural growth in known age African elephants (*Loxodonta africana*). *J. Zool. Lond.*, 236: 29 – 41.
- Marana S R, Ribeiro A F, Terra W R, Ferreira C, 1997. Ultrastruc-

- ture and secretory activity of *Abracris flavolineata* (Orthoptera: Acrididae) midguts. *J. Insect Physiol.*, 43 (5): 465 – 473.
- Modder W W D, 1984a. The attraction of *Zonocerus variegatus* (L.) (Orthoptera: Pyrgomorphidae) to the weed *Chromolaena odoratum* and associated feeding behaviour. *Bull. ent Res.*, 74: 239 – 247.
- Modder W W D, Singh S R, 1976. Utilisation of cassava, *Manihot esculenta*, in the laboratory by the later instars of the African grasshopper, *Zonocerus variegatus* (L.) (Acridoidea: Pyrgomorphidae). *Rev. Zool. Afri.*, 90: 417 – 430.
- Modder W W D, Tamu G F, 1996. The effects of food plants on metabolic reserves, development and fecundity in the African pest grasshoppers, *Zonocerus variegatus* (Linnean) (Orthoptera: Pyrgomorphidae). *African Entomology*, 4 (2): 189 – 196.
- Needham A E, 1943. On relative proportions in serially repeated structures (seriometry). 1. Limbs and body segments of *Lithobius forficatus* (L.). *Proceedings of Zoological Society of London*, 115: 355 – 370.
- Okere A N, 1980. Studies on the biology of *Zonocerus variegatus* (Linnean) (Orthoptera: Acrididae). Ph. D Thesis, University of Ibadan, Nigeria.
- Richards O W, Davies R G, 1978. Imm's Outlines of Entomology. 6th ed. Chapman and Hall London. 71 – 72.
- Shine R, Harlow P S, Keogh S S, Boedi, 1998. The allometry of the history traits: insight from a study of giant snakes (*Python reticulatus*). *J. Zool. Lond.*, 244: 404 – 414.
- Strong L, 1967. Feeding activity, sexual maturation, hormones and water balance in the female African migratory locust. *J. Insect Physiol.*, 13: 495 – 507.
- Terra W R, 1990. Evolution of digestive system in insects. *Ann. Rev. Entomol.*, 35: 181 – 200.
- Toye S A, 1982. Mini Review: Studies on the biology of the grasshopper pest of *Zonocerus variegatus* (L.) (Orthoptera: Pyrgomorphidae) in Nigeria: 1911 – 1981. *Insect Sci. Applic.*, 3: 1 – 7.
- Treherne J E, 1957. The absorption of glucose from the alimentary tract of the locust, *Schistocerca gregaria* (Forsk.). *J. exp. Biol.*, 35: 297 – 306.
- Treherne J E, 1958a. Facilitated diffusion and exchange in the absorption of glucose by the locust, *Schistocerca gregaria* (Forsk.). *Nature*, 181: 1 280 – 1 281.
- Treherne J E, 1958b. The absorption of glucose from the alimentary canal of the locust, *Schistocerca gregaria* (Forsk.). *J. exp. Biol.*, 35: 297 – 306.
- Treherne J E, 1958c. The absorption and metabolism of sugars in the locust, *Schistocerca gregaria* (Forsk.). *J. exp. Biol.*, 35: 611 – 625.
- Uvarov B, 1966. Grasshoppers and locusts. Vol. 1. Methuens, London. 1 – 10.
- Volksmann A, Peters W, 1989. Investigations on the midgut caeca of mosquito larvae 11. Functional aspects. *Tissue Cell*, 21 (2): 253 – 261.
- Worcester S E, 1995. The scaling of the size and stiffness of primary flight feathers. *J. Zool. Lond.*, 239: 609 – 624.

臭腹腺蝗（直翅目：锥头蝗科）胃盲囊的异速生长和功能特性

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摘要：通过对臭腹腺蝗 *Zonocerus variegatus*（直翅目：锥头蝗科）6个若虫期及成虫期主消化道和胃盲囊分段进行解剖和测量，对其胃盲囊的异速生长和功能特性进行了研究。结果表明，胃盲囊和主消化道的生长是不同速的。胃盲囊前段较后段生长速率更高，但两者生长速率显著相关。消化道和胃盲囊的平均长度亦显著相关。随年龄增长，消化道的生长速率降低，而胃盲囊的生长速率上升。与胃盲囊前段功能相同，胃盲囊后段亦具有消化和吸收功能，被认为能在营养缺乏的旱季起到增加肠胃吸收面的功能。

关键词：臭腹腺蝗；胃盲囊；生长速率；功能

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